
Can Arctic seabirds adapt to climate change?

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The current biodiversity crisis is, in many ways, a crisis of maladaptation. If a species is adapted to a particular habitat or niche that disappears or degrades, the species finds itself maladapted. With climate change, species must track warming across space or through time to retain a reasonable degree of adaptation and therefore persist. Ultimately, adaptive evolution *in situ* must occur in conjunction with range shifts, as abiotic/biotic conditions are unlikely to be the same in newly colonised areas. Moreover, many species may be trapped geographically by dispersal barriers or a lack of suitable habitat in which to move.

Phenotypic plasticity – the ability of a genotype, or individual, to express different phenotypes in different environments – can be an important first line of defence against maladaptation. Plasticity is unlikely, however, to result in perfect phenotypic tracking of environmental change (Gienapp, Reed, & Visser, 2014), and maladaptive responses that exacerbate the problem are also possible (Acasuso-Rivero, Murren, Schlichting, & Steiner, 2019). Only evolution in response to natural selection, which may include adaptive evolution of plasticity itself, can close the maladaptation gap. A major focus of contemporary evolutionary ecology, therefore, is to understand the relative contributions of evolution and plasticity (including the evolution of plasticity) to trait change, their influences on each other, and their contributions to population resilience in changing environments.

In this issue of *Functional Ecology*, Sauve, Divoky, & Friesen (2019) explore these issues in a high Arctic seabird, Mandt's black guillemot (*Cepphus grylle mandtii*), whose ecology is closely tied with sea-ice. The Arctic is among the fastest warming regions globally, with concomitant rapid changes in spring phenology (Berteaux, Réale, McAdam, & Boutin, 2004). At Cooper Island, Alaska, there is but a tight seasonal window for black guillemots to fit in breeding, which requires access to snow-free nest cavities. The annual timing of snowmelt has advanced by ~9 days since 1976, while the birds have advanced their clutch initiation dates (CID) by ~8 days. On the face of it, this suggests rather accurate tracking of environmental change, but we lack a yardstick for what the birds 'should be' doing, e.g. the rate at which phenology of their food (seasonal peaks in biomass of prey species) is advancing (Visser & Both, 2005). This is a common problem faced by studies where prey dynamics are challenging to monitor and animals being studied forage over large areas. Selective pressures other than matching a seasonal food peak may also be at play (Both, Van Asch, Bijlsma, Van Den Burg, & Visser, 2009; Durant, Hjermann, Ottersen, & Stenseth, 2007).

Using individual-level data, Sauve, Divoky, & Friesen (2019) showed that earlier-breeding females fledged more chicks annually and were themselves more likely to survive to the next year. This directional selection on breeding date implies population-level maladaptation: higher mean fitness would result if the birds bred earlier, suggesting they are lagging behind an optimum. The ecological drivers of this selection remain unknown, for now, but new statistical methods that allow characterisation of how optimal trait values vary with candidate environmental variables (Chevin, Visser, & Tufto, 2015) could help to shed light here. It is also possible to test indirectly for signals of trophic mismatch by exploring correlations between annual selection and relevant climate variables, and testing for temporal trends in both.

What makes this study stand out is that the authors can convincingly conclude that plasticity rather than microevolution must explain the observed advancement. They can do this because phenotype and fitness data were paired with pedigree information (a map of who is related to whom) to disentangle the relative contributions of plasticity and evolution. Phenotypic resemblance among individuals of varying relatedness can be used in an 'animal model' (Wilson et al., 2010) to infer the extent to which phenotypic (co)variation has an additive genetic basis, and thus whether traits can evolve. Surprisingly, little to no additive genetic variance (V_A) in CID was found, but an overall positive relationship between CID and annual snowmelt date was evident, implying that plasticity rather than microevolution must explain the observed advancement. A power analysis revealed sufficient statistical power to detect heritability (h^2; the ratio of V_A to phenotypic variance) as low as 0.05, giving confidence that true h^2 was indeed very low. Two other studies of long-lived birds (Charmantier, Perrins, McCleery, & Sheldon, 2005; Teplitsky, Mills, Yarrall, & Merilä, 2010) have also documented non-significant h^2 of laying date in prime-age females, yet another two (Brommer, Rattiste, & Wilson, 2008; Dobson, Becker, Arnaud, Bouwhuis, & Charmantier, 2017) found significant heritable variation. It is too early to say whether there are broad life history or ecological correlates of the magnitude of genetic variation in avian laying dates, but this warrants further study.

An alternative approach to gain insight into the capacity for populations to adapt to environmental change is to estimate V_A (or h^2) in fitness itself, which represents the total evolutionary potential of a population across all traits (Hendry, Schoen, Wolak & Reid, 2018; (Bonnet, Morrissey, & Kruuk, 2019). The downside is that one remains in the dark regarding environmental drivers of adaptation, if ecological causes of selection on particular traits are not investigated explicitly. Testing for environmental dependence of V_A for fitness itself may be an instructive, albeit data-hungry, exercise; for example, if V_A for fitness increases with temperature, this could imply a faster rate of adaptive evolution as global warming intensifies. In general, the toolkit of quantitative genetics holds great promise for understanding and forecasting evolutionary dynamics of polygenic traits – for which we may never know all the underlying genes – in complex environments (Kruuk, Slate, & Wilson, 2008).

Overall, the Sauve, Divoky, & Friesen (2019) study represents a significant advance in understanding adaptive plasticity and constraints on adaptation in extreme environments, but important questions remain. As emphasised by these authors, future work must link trait dynamics to demography, e.g. whether changes in phenology or selection patterns are associated with changes in mean (age-specific) fecundity or viability, to assess the potential consequences of future warming for population persistence. Examining phenology changes at multiple trophic levels at relevant spatial scales remains a formidable challenge in marine systems, but this is essential for understanding whether climate change is disrupting ecological interactions and what this means for the species involved. On top of these indirect effects, direct effects of future rapid warming may become a problem even for endotherms; e.g. pre-existing adaptations in high-latitude endotherms for minimising heat loss may render them vulnerable to heat stress, but there is rather little work on this (Oswald & Arnold, 2012). Finally, comparative studies of relationships among climate, phenology and natural selection (e.g. Keogan et al., 2018; Radchuk et al., 2019) can help reveal generalities, or interesting exceptions that prompt new research directions, in how species with different natural histories respond to global change.

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